THE BIOLOGY OF PERLA IMMARGINATA SAY.*

By Lucy Wright Smith.

Introduction. Perhaps less is known concerning the life-histories and habits of the Plecoptera than of any other group of aquatic insects. Hence a more extensive knowledge of stone-flies along biological lines is desirable. At the suggestion of Professor James G. Needham such a study was commenced at Ithaca in the fall of 1910.

This locality with its many creeks and spring brooks is an excellent collecting ground for Plecoptera, and the equipment of the limnological laboratory of Cornell University makes an intensive study of aquatic forms possible. The essential factor in rearing stone-flies, as in many other stream-inhabiting insects, is running water. This is provided by a series of taps in a roof garden aquarium and also in a small artificial pond out of doors.

Methods. With the hope of obtaining truer results by keeping conditions as natural as possible, most of this study is being carried on out-doors. Some care must be taken in transporting stone-fly nymphs from the stream to permanent quarters. Full grown nymphs can breathe air directly, and have been carried most successfully wrapped in a wet cloth or packed in damp moss. Smaller nymphs can be taken safely for short distances in collecting jars full of clean, cold water.

In the artificial pond the nymphs are kept, eight to ten together, in cylindrical cages made of galvanized wire screen with cheese cloth covers. For small nymphs it is necessary to have the lower part of the cage lined with cloth. The cages are partially submerged in the current near the taps. With flat stones and bits of water weed in the bottom, and a steady flow of water, the nymphs can live a natural life.

The shyness of adult stone-flies makes field observations at close range impossible. Consequently they are kept in screen cages of about two by three feet. Here again an imitation of natural environment is attempted. This is done by keeping green twigs, clumps of sod, stones and pans of water in the cages.

*Contribution from the Limnological Laboratory of Cornell University.

Although these pans of water are but a poor imitation of streams they suffice for most purposes. Better aerated water is necessary, however, for development of eggs. For this reason they are kept in running water in test-tubes closed at either end with fine silk bolting-cloth.

Nymph.

Habitat. This introductory paper includes only the observations made in June, July and August of the past summer, upon a single species, Perla immarginata. The nymphs occur in moderate numbers in all the larger streams about Ithaca, and very abundantly in the spring brook at Coy Glen. This abundance may be accounted for by the fact that there is less competition for a livelihood in this stream. Perla immarginata reigns supreme at the height of its season, the middle of July, not only as the largest of the stone-flies, but of all the aquatic insects. In the other streams are several competitors of equal size and strength and many more enemies.

Early in the spring, torrents of water rush through the glen, but in July and August the brook is reduced to a shallow stream. The high walls and the narrow, winding course of the gorge shut out so much sun-light that in spite of its shallowness, the water is always cold. Much of the stream bed is shale, free from sand and gravel, but well covered with a diatomaceous ooze. Here the water flows in a thin sheet. In other places are deeper pools strewn with clean, coarse gravel. Stones of all shapes and sizes are scattered along the stream. At this season, most of the stones, even the flat ones on the rocky bed, are partly out of water. Generally these are the haunts of stone-fly nymphs just before emergence.

Neighbors and enemies. These same stones shelter other creatures, fragile may-fly nymphs, chironomid larvae partially concealed in their slime tubes, and caddis worms standing guard behind their seines. Nearby on the rough floor of the stream hang the last stragglers of the mats of black fly larvae. In crevices on all sides lurk cray-fish, less welcome neighbors.

Occurence. Late in June an occasional sprawling, nymphal skin clinging to the upper surface of a stone fortells the approach of the season for Perla immarginata. About three weeks later the casts are very numerous, and the overturning of a single stone sends a whole colony of the tiger-striped nymphs scampering in all directions in search of hiding places.

Length of Nymphal Life. It is evident at a glance that these nymphs are not all of the same size or stage of development. They fall into three groups. One contains very few individuals, these are small immature nymphs not more than half an inch in length. The second group, also a small one, is made up of nymphs about three quarters of an inch long. These are immature too, but older than first, larger and with small wing pads. The mature nymphs with their black wing pads form the largest group.

As far as is known, the complete life-history of no stone-fly has been worked out. Therefore we can only speculate concerning the length of it, knowing of course that whatever it may be, by far the greater part is spent in the nymphal stage. From the brief period of incubation of the eggs of some of the smaller individuals of the group, Capnia for example, and from the appearance of mature nymphs only at the emerging season, it seems probable that the life-history of these is completed in a year. On the other hand, the three groups of nymphs of different size in Perla immarginata and allied species, seem to indicate, as in some of the larger may-flies, a longer period, probably three years. Just where the nymphs live when it is not the transformation season, is not known.

Adaptations. A closer examination of the mature nymph shows that there are no external sexual characters. Nevertheless, the females can be easily separated from the males because the dark brown eggs show through the sides of the abdomen. In addition, as one would expect, the males are smaller; they vary from three quarters of an inch to an inch in length. The females have the same degree of variation, the largest being about an inch and a quarter in length and the smallest a little less than an inch. The color pattern of the nymph, black banded with white or pale yellow, and snowy white tufts of the tracheal gills on the thorax behind and above each leg, would make them rather conspicuous if they lived in the open. (Figs. 3 and 4).

The form of the nymph—flat-bodied, with flat, sprawling legs, and tarsi armed with two strong claws—is strikingly adapted for clinging. The legs are fringed with long hairs, which make them useful in swimming as well as running, and one need only disturb the nymphs to see how swiftly they can escape by either method. The shyness of stone-fly nymphs, their splendid

adaptations for clinging, running and swimming make their existence fairly easy, especially in this stream where the crayfish is the only enemy of any account.

Food Habits. The long standing supposition that stone-fly nymphs devour their weaker neighbors, has been confirmed for this species in a study of their food habits. This has been done by examining the stomach content of nymphs taken from the stream, and also by feeding those in captivity. Dissections of mature nymphs show the alimentary canals empty and in many cases even so collapsed that they are difficult to find at all. Likewise the nymphs kept for rearing refused all food for eight or ten days before transformation.

With growing nymphs it is different; here it is a task to supply them with enough food to prevent their eating one another. In a single day three or four of these nymphs will dispose of a score or more black-fly larvae and half as many small may-fly nymphs. Their greed is brought out even more strikingly by examining the food mounts of nymphs taken from the stream; whole specimens of midge larvae are found not uncommonly and sometimes a may-fly nymph with even the gills intact. The mass of food, however, consists of innumerable shapeless scraps of chitin with scattered fragments of abdomens, setae, antennae, legs; or claws, whole heads, mandibles, maxillae, and labia, making possible the recognition of may-fly and stone-fly nymphs, midge and simulium larvae and pupae.

The only evidence of any herbivorous tendency in this species is the presence of an immense number of diatoms in food amounts. Of course this is a question of direct or indirect eating. One would expect to find diatoms in a food mount made up of pieces of may-fly nymphs and chironomid larvae, and the natural supposition might be that the stone-fly got them second hand. Yet such a statement cannot be made without some hesitation, because the number of diatoms in the mounts seems to increase with a general decrease in the amount of food; and also because diatoms have been found to be the chief food of some of the smaller species of stone-flies.

Transformation. Just before the time of transformation when the nymphs cease eating they become sluggish. And as the time approaches they crawl further and further toward the surface of the water, and finally entirely out of it where they often remain for hours before emergence. The actual

casting of the skin has not been seen in this species. Although adults are rarely absolutely perfect specimens, the percent of individuals lost by inability to complete transformation is exceedingly small. Judging from the fact that no newly emerged insects have been found, it is thought that they must transform during the night, or more probably, in the early hours of the morning.

Adults.

Characteristics. The adult Perla immarginata, (Fig 5), is uniformly dull brown and much less conspicuous than the nymph. As soon as the insect loses its tracheal gills and gains four well developed wings, it is ready for aerial life. Unlike many adults with this equipment, some of the nymphal tendencies are carried over into this stage. Chief among these is the love for hiding. So great is their shyness that, even at the height of the emerging season, the adults are rarely found in the field. Repeated attempts at sweeping the foliage along the stream have met with little success. Careful searching of the rocky walls of the gorge has occasionally revealed an adult hidden away in a crack or crevice. Similar habits have been noticed in the adults kept in cages. They never rest on the twigs but crawl into hiding under the edge of the stones, or pans, or wherever they can wedge themselves into a tight place.

Although they avoid day-light, artificial lights attract them at night. They have been found crawling along poles and fences, or in the road under electric lights in the neighborhood of streams.

When disturbed the adults rarely seek escape by flight, but usually by running. Here again we see a nymphal trait, and a characteristic of the group. They are poor flyers and dependent upon their legs. Some stone-flies do not fly at all, although provided with fully developed wings.

Food Habits. A striking difference between the nymph and adult is found in the structure of the mouth and in the food habits. A character long assigned to stone-flies is rudimentary mouth parts of a biting type. This is true for Perla immarginata, but not for the entire order. In this species we have the reduction of the strong chitinous mandibles to mere fleshy lobes, (Fig. 1). The very appearance of such an apparatus indicates its uselessness, and examination of the

alimentary canal of adults taken in the field, has confirmed this. Water seems much more essential than food for these adults. If ever found out of hiding in their cages, they were almost sure to be on the stones in the pans with their mouths buried in water. Entirely deprived of water, the average length of life is shortened by several days.

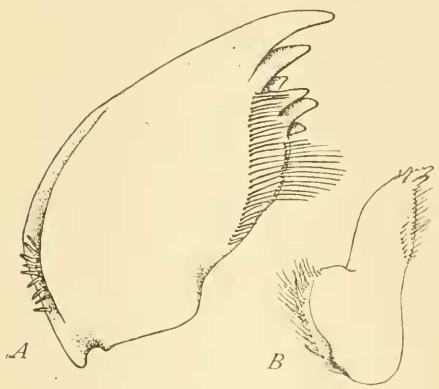

Fig. 1.

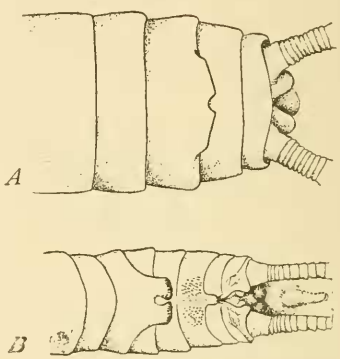

Fig. 2.

Fig. 1.

a. Left mandible of the nymph, inner surface.
b. Left mandible of the adult, same view and magnification.

Fig. 2.

a. Abdomen of the female, ventral view showing the modification of the eighth sternite.
b. Abdomen of the male, dorsal view showing the genital armature with the penis extruded.

Both figures drawn to the same scale.

The voraciousness of the nymphs is necessary, since the adults abstain from food and since enough energy must be stored up to last through aerial life and the completion of the final function, reproduction.

Mating. Ordinarily mating begins soon after emergence. The readiness with which it takes place in captivity has been a great surprise on account of the natural timidity of stone-flies. Frequently pairs have been found in copula in the breeding cages and have been removed to adult quarters without arousing enough alarm to cause their separation. By careful manipulation copulating pairs can even be held in the palm of the hand. This has made a detailed study of mating possible.

Difference in size and external sexual characters make distinguishing the sexes easy. The smallest males measure not more than an inch to the tip of the wings, and the greatest measurement for a female is one and three-fourths inches. In the female the posterior border of the eighth sternite is thickened and slightly emarginate in the middle, (Fig. 2, A). The external sexual appendages of the male, although hidden by the wings, are much more prominent. The fifth tergite is prolonged in the form of a fork extending over the sixth and most of the seventh tergites. The tip of this meets a groove running through the mid dorsal line on the eighth, and surrounded on either side by papillose prominences. The ninth segment is shortened, and the tenth is slightly elongate ending in two strong recurved hooks, (Fig. 2, B).

Just how such an apparatus operated was not obvious at first or even second glance, in fact not until copulation was actually seen. The male rests upon the female grasping her wings and abdomen with the legs of one side, and supporting himself with the legs of the other side. Then bending the end of the abdomen around that of the female, and arching it forward, the male presses close against the female and pulls down the lamina, forcing the recurved hooks up into the vagina. After a few seconds, the male starts a slightly rythmic motion by alternately pulling to and fro. As the motion becomes greater, the hooks are gradually withdrawn, and there is exposed between them a white, fleshy penis resting in the groove and supported toward the tip, by the fork on the fifth tergite. This rythmic motion seems to be pump-like in action. With a quick jerk the recurved hooks are brought up against the fork, an act which causes the contraction of the penis and forces the seminal fluid up into the vagina. The expansion is slower, allowing the penis to become refilled. Undisturbed, copulation usually lasts about forty-five or fifty minutes. Except for microscopic horny papillae on the tip, the penis is entirely fleshy and composed of two telescopic segments. After copulation, it is gradually retracted into the body just below the anal opening, and entirely hidden inside.

Egg-laying. As is commonly known, stone-flies do not deposit their eggs directly, but carry them around for a time in a mass at the end of the abdomen. It is hard to see the reason for this. Apparently it is not to be found in the condition of

the egg itself, for there seems to be no difference between eggs just extruded and those carried for a couple of hours, half a day, or longer. There is a constant regularity in the length of time that elapses between copulation and extrusion of eggs, but not in the length of time eggs are carried. Individuals in the same cage eventually deposit their eggs in the same place, but one may carry them two hours, and another nearly a day under exactly the same conditions.

I am in doubt as to the normal method of depositing eggs. In the field, smaller species, carrying eggs, are often seen on the stones in streams as if they were about to crawl down to the water. And again they appear flying low along the stream and dipping to the surface as if ovipositing. No such observations have been made upon the larger species. The few adults of Perla immarginata which have been seen dropping their eggs in the pans seemed to do it more from accident than from intention. They were crawling around the stones and had floundered into the water. The instant they came in contact with the water the eggs dropped to the bottom of the pan. But many masses of eggs have been found in the pans too far from the edge, or from the stones, for them to have been dropped except from above, or by the individuals having actually crawled into, or on the water.

Concerning the place where the eggs are deposited there is no doubt. When the globular mass touches the water the eggs begin to separate. In the pans they finally settle down into a patch one layer deep, (Fig. 6). Of course this is not the case in the streams where the current scatters them broadcast. They are not tossed about long, however, for as soon as they come in contact with any object they become attached by the glutinous cap which surrounds the micropylar apparatus. These eggs are about half a millimeter long, dark brown in color and oval-shaped. Except for a single circular ridge the chorion is without ornamentation, (Fig. 7).

In following the movement of the different adults from day to day it was necessary to have some means of identifying them as individuals. As has been previously stated, an absolutely perfect adult is rare. Consequently it was a very simple matter to recognize individuals on such characters as a broken antenna or seta, a tarsus minus a segment or two, an imperfect wing, and so on. In this way during the season thirty-two

females and twelve males were kept under close observation. It was soon found that all the eggs were not deposited at one time. A few hours after the first mass was laid, mating occurred again, and within twenty-four hours a second lot had been deposited. Often there was a third mass, and in a few instances a fourth. These followed less rapidly.

As one would expect each successive mass was smaller than the one preceding. A thousand eggs is ample average for a first mass and four masses together would not total over sixteen hundred. It seems likely that a large number of eggs must reach the hatching stage. The chances of fertilization are good since copulation occurs more than once, also if one mass has fallen in an unfavorable place there is a possibility that the others have met with better luck. Yet the number of individuals which reach maturity is comparatively small. A great loss probably occurs during the early nymphal stage when the small white nymphs would be dainty morsels for many a larger creature.

Mating has the usual effect upon the length of life of the adults. When males and females are caged together the average female dies after six or seven days and the male after nine or ten. On the other hand if the sexes are kept apart they live twelve or thirteen days.

Only a small proportion of the eggs laid in captivity were kept for development. These were easily loosened from the pan with a pipette, removed to the glass tubes and put into running water. They have not yet hatched.

Ordinarily the one great difficulty which has stood out above all others, in attempting to get a complete life history of a stone-fly has been in the handling of the very young nymphs. Although a variety of methods have been tried, nymphs have not been kept alive for longer than ten days. Whether this is due to lack of proper environment, the right kind of food, or both, can not be said. The only possibility of tracing the life-cycle of a stone-fly, from egg to adult, seems to hinge upon a more complete knowledge of the early nymphal life.

PLATE XXIII.

Fig. 3. Dorsal view of the nymph, natural size.
Fig. 4. Ventral view of the nymph, natural size.
Fig. 5. Adult female, natural size.
Fig. 6. Mass of eggs, about 4 times natural size.
Fig. 7. A single egg, greatly enlarged.